

Liparis macrosepala (Orchidaceae), a new species from southwest China with its phylogenetic position

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Abstract

A new orchid species, *Liparis macrosepala*, is illustrated and described from Yunnan Province, China, based on morphological and molecular analyses. This plant is characterised by the ovoid-fusiform, slightly compressed pseudobulbs with 4 or 5 leaves with slightly crisped margins on their apical half, dorsal sepal heart-shaped, lip with a bituberculate basal callus and a thickened folded lateral lobe on each side, centrally with one cavity with slightly raised margins, the column with a single pair of broadly triangular, obtuse wings. Maximum Likelihood and Bayesian Inference analyses of combined nrITS and plastid *matK* DNA sequences place this species in section *Cestichis*.

Keywords

Liparis section *Cestichis*, molecular phylogeny, morphology, *matK*, nrITS

Introduction

The genus *Liparis* Rich. (Epidendroideae, Malaxideae, Malaxidinae) comprises about 320 species distributed worldwide with more than 70 species in China (Pridgeon et al. 1999; Chen et al. 2009; Tian et al. 2015; Huang et al. 2018; Ya et al. 2021). Species

from this genus are terrestrial, lithophytic, epiphytic and rarely mycoheterotrophic, with inflorescences laxly or densely many-flowered, lip often reflexed and usually with a basal callus, lacking a spur, column winged at apex and sometimes at base and four pollinia in two pairs (Chen et al. 2009).

During our field surveys in Xishuangbanna, Yunnan, China, an unknown species was found. In this paper, we analysed the morphological differences of the newly-found species and its allied species and the phylogenetic position of the new entity is also discussed, based on molecular evidence from nrITS and plastid *matK*. After careful morphological comparison and phylogenetic analyses, we concluded that this species is new to science.

Material and method

Morphological observations

Materials of the new species were collected from Xishuangbanna, Yunnan, China during a field expedition. Morphological characters were observed, measured and photographed based on five living individuals under a stereomicroscope (SZX16-6151, Olympus, Japan) and photographed with a digital camera (D750, Nikon, Japan). A voucher specimen, designated as the holotype, was deposited at Shanghai Chenshan Herbarium (CSH). Conservation assessment has been conducted following IUCN guidelines (IUCN 2019).

Taxonomic sampling

DNA sequences of nrDNA ITS and plastid *matK* of the new species were sequenced and sequences of the same markers for 82 related species were downloaded from GenBank, including five outgroup species from other subtribes (Table 1).

Phylogenetic analyses

DNA sequences were aligned using the MAFFT programme in Geneious v. 2020.2.4 (<https://www.geneious.com>, accessed on 10 March 2021). Phylogenetic analyses were conducted using Maximum Likelihood (ML) and Bayesian Inference (BI) in RAxML v.7.0.4 (Stamatakis 2006) and MrBayes v.3.2.6 (Huelsenbeck and Ronquist 2001; Ronquist et al. 2012), respectively. The appropriate DNA substitution model under AIC criteria was estimated using jModelTest 2.1.10 (Posada 2008). ML analyses were conducted with bootstrap values calculated by running 1,000 replicates. For BI analysis, four chains were run with random initial trees, each for 1,000,000 generations, until the average standard deviation of the split frequency values was less than 0.01 to ensure convergence, sampling trees every 1,000 generations. After the first 20% of samples were discarded as burn-in, the remaining replicates were used to estimate the posterior probabilities.

Table I. Taxon sampling in this study.

	Species Name	nrITS	matK
1	<i>Acanthophippium mantinianum</i> L.Linden & Cogn.	AF521081	AF263618
2	<i>Collabium simplex</i> Rchb.f.	EF670387	AY557200
3	<i>Crepidium acuminatum</i> (D.Don) Szlach.	KJ459274	KJ459304
4	<i>Crepidium bahanense</i> (Hand.-Mazz.) S.C.Chen & J.J.Wood	MH116611	MH117500
5	<i>Crepidium bancanoides</i> (Ames) Szlach.	AB290885	AB290893
6	<i>Crepidium brevidentatum</i> (Schweinf.) M.A.Clem. & D.L.Jones	AB290886	AB290894
7	<i>Crepidium resupinatum</i> (G.Forst.) Szlach.	JN114483	JN004403
8	<i>Dendrobium dixanthum</i> Rchb.f.	KY966535	KY966825
9	<i>Dienia cylindrostachya</i> Lindl.	JN114491	JN004422
10	<i>Eria ferruginea</i> Lindl.	AF521071	AF263660
11	<i>Eulophia graminea</i> Lindl.	MH768269	MH767976
12	<i>Liparis macrosepala</i> Z.W. Wang, Y. Zhang & W.C. Huang	ON642332	ON642331
13	<i>Liparis anopheles</i> J.J.Wood	AY907075	AY907139
14	<i>Liparis assamica</i> King & Pantl.	KJ459276	KJ459306
15	<i>Liparis aureolabella</i> J.D. Ya & Z.D. Han	MN065679	MN065733
16	<i>Liparis auriculata</i> Blume ex Miq.	AB289458	KF262076
17	<i>Liparis balansae</i> Gagnep.-1	KF589874	KF589880
18	<i>Liparis balansae</i> Gagnep.-2	KJ459277	KJ459307
19	<i>Liparis bingzhongluoensis</i> X.H. Jin	MW169041	MW169042
20	<i>Liparis bistriata</i> E.C.Parish & Rchb.f.	KJ459279	KJ459309
21	<i>Liparis bootanensis</i> Griff	KJ459280	KJ459310
22	<i>Liparis bracteata</i> T.E.Hunt	AY907076	AY907140
23	<i>Liparis brunnescens</i> Schltr.	AY907098	AY907165
24	<i>Liparis condylobulbon</i> Rchb.f.	AY907080	AY907144
25	<i>Liparis cordifolia</i> Hook.f.	KJ459282	KJ459312
26	<i>Liparis delicatula</i> Hook.f.	KJ459283	KJ459313
27	<i>Liparis distans</i> C.B.Clarke	KJ459284	KJ459314
28	<i>Liparis disticha</i> (Thouars) Lindl.	AY907081	AY907145
29	<i>Liparis elliptica</i> Wight	KJ459285	KJ459315
30	<i>Liparis fissilabris</i> Tang & F.T.Wang	KJ459286	KJ459316
31	<i>Liparis fissipetala</i> Finet	KJ459287	KJ459317
32	<i>Liparis formosana</i> Rchb.f.	AY907082	AY907147
33	<i>Liparis fujisanensis</i> F.Maek. ex Konta & S.Matsumoto	EU024936	EU024937
34	<i>Liparis gibbosa</i> Finet-1	AY907083	AY907148
35	<i>Liparis gibbosa</i> Finet-2	AY907084	AY907149
36	<i>Liparis glossula</i> Rchb.f.	KJ459289	KJ459319
37	<i>Liparis guangxiensis</i> C.L.Feng & X.H.Jin	KF589875	KF589881
38	<i>Liparis japonica</i> (Miq.) Maxim.	AY907086	AY907151
39	<i>Liparis koreana</i> (Nakai) Nakai	EU017422	EU017444
40	<i>Liparis kumokiri</i> F.Maek.	AY907087	AY907152
41	<i>Liparis latifolia</i> Lindl.	AY907088	AY907153
42	<i>Liparis latilabris</i> Rolfe	KJ459291	KJ459321
43	<i>Liparis liliifolia</i> (L.) Rich. ex Lindl.	AY907090	AY907156
44	<i>Liparis loeselii</i> (L.) Rich.	AY907091	AY907157
45	<i>Liparis makinoana</i> Schltr.	EU017405	EU017428
46	<i>Liparis mannii</i> Rchb.f.	KJ459293	KJ459323
47	<i>Liparis meihuashanensis</i> S.M.Fan	MF959772	MF959773
48	<i>Liparis mengziensis</i> J.D. Ya & Lei Cai	MN065734	MN065678
49	<i>Liparis nanlingensis</i> H.Z.Tian & F.W.Xing	AB701346	/
50	<i>Liparis napoensis</i> L.Li, H.F.Yan & S.J. Li-1	MT012899	MT019986
51	<i>Liparis napoensis</i> L.Li, H.F.Yan & S.J. Li -2	MT012900	MT019987
52	<i>Liparis nervosa</i> (Thunb.) Lindl.	AY907092	AY907158
53	<i>Liparis nugentiae</i> F.M.Bailey	AY907093	AY907159
54	<i>Liparis odorata</i> (Willd.) Lindl.	KJ021033	KJ021029
55	<i>Liparis pandurata</i> Ames	AY907094	AY907160
56	<i>Liparis pauliana</i> Hand.-Mazz.	AY907096	AY907163

	Species Name	nrITS	matK
57	<i>Liparis petiolata</i> (D.Don) P.F.Hunt & Summerh.	MW186826	MW187482
58	<i>Liparis resupinata</i> Ridl.	KJ459297	KJ459327
59	<i>Liparis somae</i> Hayata-1	MT012898	MT019985
60	<i>Liparis somae</i> Hayata-2	MT012897	MT019984
61	<i>Liparis sootenzanensis</i> Fukuy.	KJ021034	KJ021030
62	<i>Liparis stricklandiana</i> Rchb.f.-1	MT012903	MT019990
63	<i>Liparis stricklandiana</i> Rchb.f. -2	KJ459298	KJ459328
64	<i>Liparis sula</i> N.Hallé	AY907104	AY907171
65	<i>Liparis terrestris</i> J.B.Comber	AY907105	AY907172
66	<i>Liparis truncicola</i> Schltr.	AY907106	AY907173
67	<i>Liparis viridiflora</i> (Blume) Lindl.-1	MT012902	MT019989
68	<i>Liparis viridiflora</i> (Blume) Lindl.-2	MT012901	MT019988
69	<i>Malaxis brachypoda</i> (A.Gray) Fernald	AY907108	AY907175
70	<i>Malaxis monophyllos</i> (L.) Sw.	MW181626	MW187483
71	<i>Malaxis soulei</i> L.O.Williams	AY907119	AY907186
72	<i>Malaxis abieticola</i> Salazar & Soto Arenas	AY907129	AY907196
73	<i>Oberonia acaulis</i> Griff.	KY242066	KY241943
74	<i>Oberonia brunonianana</i> Wight	JN114623	JN004516
75	<i>Oberonia equitans</i> (G.Forst.) Mutel	AY907130	AY907198
76	<i>Oberonia heliophile</i> Rchb.f.	AY907131	AY907199
77	<i>Oberonia iridifolia</i> Roxb. ex Lindl.	AY907132	AY907200
78	<i>Oberonia mucronata</i> (D.Don) Ormerod & Seidenf	JN114640	JN004534
79	<i>Oberonia neocaledonica</i> Schltr.-1	AY907133	AY907201
80	<i>Oberonia neocaledonica</i> Schltr.-2	AY907134	AY907202
81	<i>Oberonia padangensis</i> Schltr.	AY907135	AY907203
82	<i>Oberonia wappeana</i> J.J.Sm.	AY907138	AY907206
83	<i>Oberonioides pusillus</i> (Rolfe) Marg. & Szlach.	KJ527610	KJ459302

Results

Phylogenetic analyses

The length of nrITS matrix was 792 bp including 262 parsimony-informative sites and for matK, the length and parsimony-informative sites were 1443 bp and 120, respectively. Both analyses (MP and BI) recovered similar relationships. The ML tree with bootstrap percentages, on which the posterior probabilities from the BI analysis were also indicated, is shown in Fig. 1.

The phylogenetic analyses indicate that *Liparis* is not monophyletic, being mingled with species of other genera of Malaxideae. This result agrees with what was found in previous studies (Cameron 2005; Margońska et al. 2012; Tang et al. 2015; Li et al. 2020; Kumar et al. 2022). The new species, henceforth referred to as *Liparis macrosepala* Z.W. Wang, Y. Zhang & W.C. Huang, is grouped with species in *Liparis* sect. *Cestichis* Thouars ex Pfitzer as the sister of a clade consisting of *L. delicatula* Hook.f., *L. fissipetala* Finet, *L. assamica* King & Pantl. and *L. resupinata* Ridl.

Morphological comparisons

Liparis is defined as species with racemose inflorescences, resupinate lip lacking a spur, column without a conspicuous foot and four pollinia in two pairs with small viscidium, but no caudicle. The morphology of *Liparis macrosepala* is in

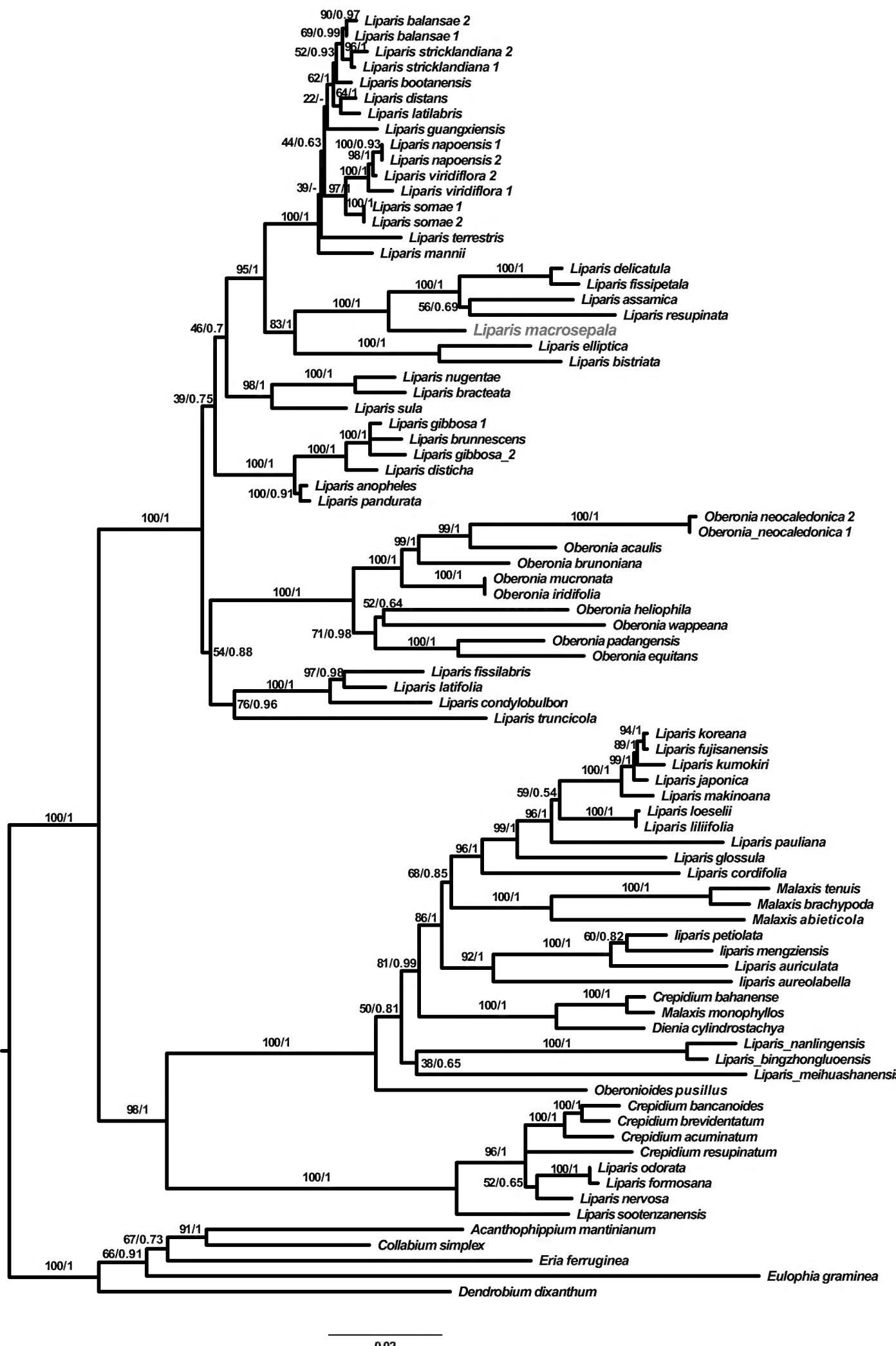


Figure 1. Maximum Likelihood tree of *Liparis* and its allied genera in subtribe Malaxidinae inferred from the combined analysis of nrITS and *matK*. ML bootstrap values (ML_{BP})/Bayesian posterior probabilities (PP) are indicated above the branches, respectively. The sectional taxonomy of *Liparis* follows Garay and Romero-Gonzalez (1999) and Li et al. (2020).

accordance with the characteristics of sect. *Cestichis* like the slightly flattened, narrowly winged rachis with alternating bracts. The morphological characters can distinguish *Liparis macrosepala* from its close relatives *L. delicatula*, *L. fissipetala*, *L. assamica* and *L. resupinata*.

Taxonomic treatment

Liparis macrosepala Z.W. Wang, Y. Zhang & W.C. Huang, sp. nov.

urn:lsid:ipni.org:names:77306143-1

Figs 2, 3

Chinese name: 大萼羊耳蒜

Type. CHINA. Yunnan Province (云南), Xishuangbanna (西双版纳), Mengla County (勐腊县) epiphyte on the tree trunk, 1620 m elev., 23Nov 2021, Zhengwei Wang, Xiaochen Li, Yu Zhang& Zhijin Wu, WZW04247 (holotype: CSH!).

Diagnosis. *Liparis macrosepala* is characterised by the ovoid-fusiform, slightly compressed pseudobulbs with 4 or 5 alternate leaves on their apical half, these with slightly crispate margins, dorsal sepal ovate with cordate base, broadly elliptic, ca. 4 mm long, 2 callus-shaped and thickened folds, base with 2 oblong lobes on both sides, centrally with 1 thickened, concave callus, column with a single pair of arcuate wings.

Epiphytic herbs. Roots slender, flexuose. Pseudobulbs clustered, ovoid-fusiform, slightly compressed laterally, 1–2 × 0.5–1 cm, upper half with 4–5 widely spaced leaves. Leaf blade ovate-oblong, 1.8–2.3 × 0.8–1.2 cm, apex acuminate, base contracted into a short petiole, articulate, margins of their apical half slightly crispate. Peduncle 7–10 cm long, with several sterile bracts 2–5 mm long; raceme with 7–10 flowers arranged in zigzag manner. Floral bracts broadly ovate with cordate base, 2–3 × 1–1.5 mm, acute. Flowers greenish-orange; pedicel and ovary ca. 7 mm long. Dorsal sepal broadly ovate with cordate base, 3.2–5 × 3–3.6 mm, 1-veined, abaxially carinate, apex acute; lateral sepal oblong-ovate or ovate-lanceolate, 5–6 × ca. 0.6 mm long, abaxially slightly carinate. Petals narrowly linear, 3–4 × ca. 0.2 mm; lip elliptic, 2–3 × ca. 1 mm, apex apiculate, base bearing a bituberculate callus, then expanded on each side into a thickened, folded, rounded lobe, with 1 excavation with raised margins between the lobes. Column straight, ca. 2 mm long, with a pair of subtriangular, obtuse wings on each side near the middle and a ridge on the back of the column. Anther cap hemispherical, pale yellow; pollinia 4 in 2 pairs with one pollinium of each pair smaller than the other, waxy, brownish, with minute apical viscidium.

Phenology: Flowering in November–December.

Distribution and habitat. It is found on tree trunks on a limestone ridge-top evergreen broad-leaved forest at an elevation of 1500–1700 m in Mengna County, Xishuangbanna Autonomous Prefecture, Yunnan Province, People's Republic of China. The habitat presents a tropical monsoon climate.

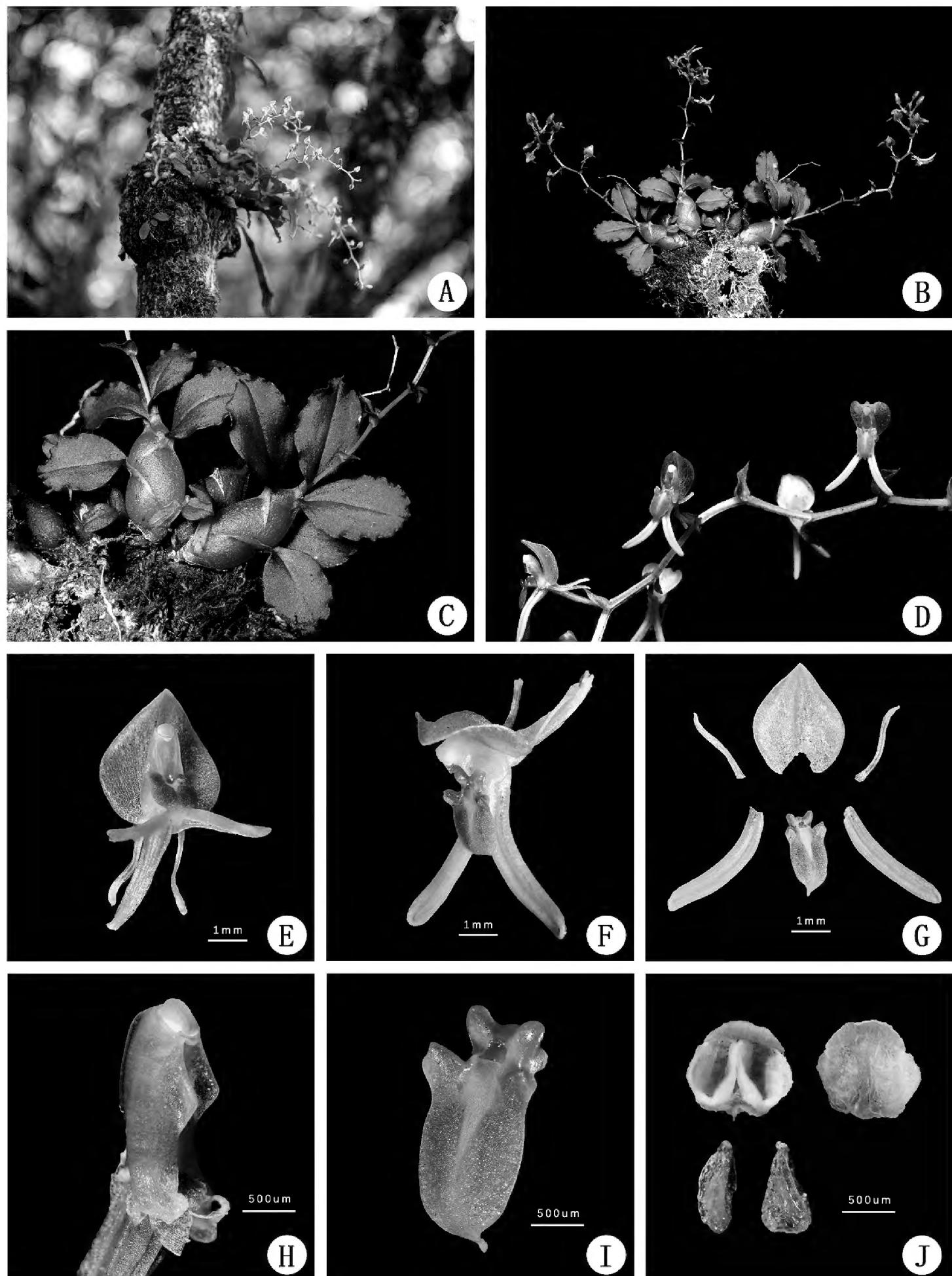


Figure 2. Morphology of *Liparis macrosepala*. **A** plants in situ **B** flowering plant **C** pseudobulbs and leaves **D** inflorescence **E** flowers, front view **F** flowers, side view **G** perianth dissection **H** column from side **I** lip in oblique view **J** anther cap and pollinia. Photographs by Weichang Huang.

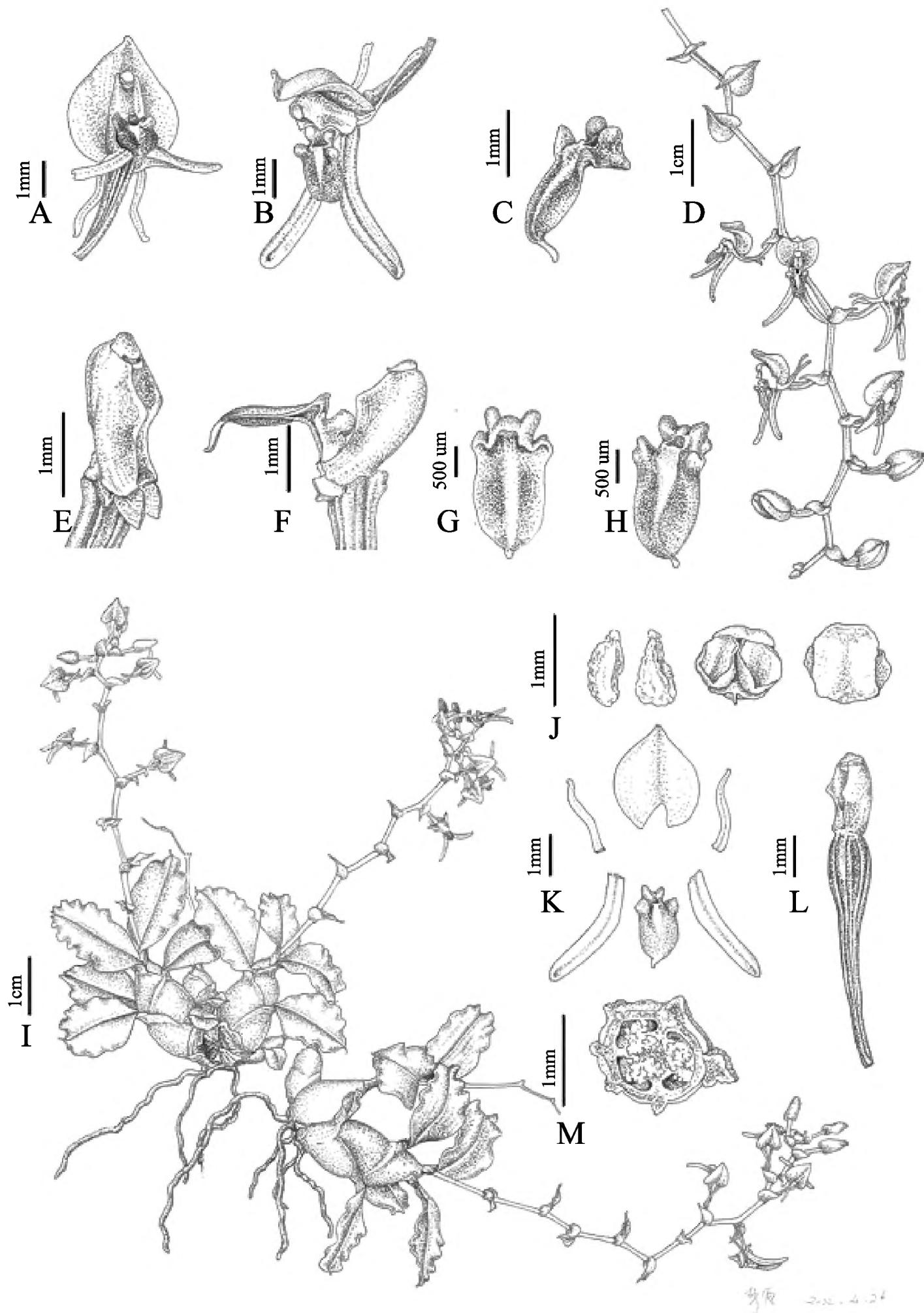


Figure 3. *Liparis macrosepala* **A** flower, front view **B** flower, side view **C** lip, side view **D** inflorescence **E** column, side view **F** lip and column, side view **G** lip, back view **H** lip, front view **I** flowering plant **J** pollinia and anther cap **K** perianth dissection **L** column and ovary, oblique view **M** ovary, transection. Drawn by Lan Yan.

Etymology. The species epithet refers to the large and conspicuous dorsal sepal of the flower.

Taxonomic notes. *Liparis macrosepala* differs from *L. delicatula* in its 4 to 5 leaves with slightly crisped margins on their apical half and single pair of wings on the column. Its entire, not Y-shaped petals and sessile lip (i.e. without a claw) easily distinguish *L. macrosepala* from *L. fissipetala*. The dorsal sepal of *L. assamica* is narrowly ovate-oblong, in contrast with the heart-shaped dorsal sepal of *Liparis macrosepala*. *Liparis resupinata* is distinguished from *L. macrosepala* by its 10–50-flowered raceme and the column with a single pair of broad wings, each with a retrorse thread. The main differences between these closely-related species, according to our phylogenetic analyses, are summarised in Table 2.

Conservation assessment. The new species was found in a ridge-top evergreen broad-leaved forest on a limestone mountain. Despite numerous surveys in the areas, only six mature individuals were found without fruits or evidence of cross-pollination.

This extremely small effective population occurs in a touristic zone which is a serious threat to the survival of the species. Consequently, the species can be assessed as Critically Endangered (CR, D), based on current information and following IUCN guidelines (IUCN 2019).

Table 2. Comparison of *L. macrosepala* and related species.

Characters	<i>L. delicatula</i>	<i>L. fissipetala</i>	<i>L. assamica</i>	<i>L. resupinata</i>	<i>L. macrosepala</i>
Pseudobulbs	oblong or cylindrical-fusiform 5–9 × 3–5 mm	ovoid, 8–10 mm long	ovoid-fusiform, slightly compressed 1.5–2.5 cm × 6–10 mm	subcylindrical or ± spindle-shaped, 1.8–5 cm × 3–6 mm	ovoid-fusiform, slightly compressed, 1–2 cm × 0.5–1 cm
Leaf	2 or 3, margin flat	3 or 4, strongly crisped-margined	3 or 4, apical half slightly crisped-margined	3 or 4, margin slightly serrate	4 or 5, apical half slightly crisped-margined
Scape	2–5 cm, several to 10-flowered, flowers white	5–10 cm long, with 10–15 flowers, flowers yellow,	10–13 cm, more than 10-flowered, flowers orange	7–18 cm, 10–50-flowered, flowers pale green or greenish-yellow	7–10 cm, more than 10-flowered, flowers greenish-orange
Bracts	ovate-lanceolate, 2–3 mm	ovate-lanceolate, 1.5–3.5 mm	lanceolate, 2–3 mm	lanceolate, 3–5 mm	broadly ovate, 2–3 mm
Dorsal sepal	ovate-oblong, 2.5–3 × 1.5–1.8 mm	oblong-lanceolate, 3–4 × 0.8–1 mm	narrowly ovate-oblong, 4.8–5.8 × ca. 1.6 mm	oblong or elliptic-oblong, ca. 4 × 1.8 mm	broadly ovate, ca. 3.2–5 × 3–3.6 mm
Petals	narrowly linear-lanceolate, 2.5–3 × ca. 0.5 mm, entire	narrow linear, 4–5 mm long, Y-shaped	narrowly linear, 5–5.5 × ca. 0.7 mm, entire	narrowly linear, ca. 3.5 × 0.3 mm, entire	narrowly linear, 3–4 × ca. 0.2 mm, entire
Lip	broadly elliptic or orbicular, ca. 2.5 mm, base with an orbicular, auriculate, callus-shaped fold on either side, with a concave callus near base	epichile broadly oblong or subsquare, 1.5–2 × 1–1.5 mm, base with two auricles on both sides; claw short, with a fleshy callus centrally near base	broadly obovate-oblong, ca. 4 × 2.7 mm, with two callus-shaped thickened folds, two suborbicular lobes on both sides, centrally with one concave callus near base	broadly elliptic-oblong or broadly ovate-oblong, 2.5–3 mm, with two lateral splits below middle; two suborbicular lobes, centrally with one bilobed callus near base	broadly elliptic, ca. 2–3 mm long, two callus-shaped and thickened folds, base with two oblong lobes on both sides, centrally with one bituberculate callus near base
Column	ca. 2.2 mm, two pairs of wings	ca. 1.5 mm, broadly winged with two horn-like appendages	ca. 2 mm, two pairs of wings	ca. 2.8 mm, a pair of wings, each with a retrorse thread	ca. 2 mm, a single pair of subtriangular wings

Acknowledgements

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References

Cameron KM (2005) Leave it to the leaves: A molecular phylogenetic study of Malaxideae (Epidendroideae, Orchidaceae). *American Journal of Botany* 92(6): 1025–1032. <https://doi.org/10.3732/ajb.92.6.1025>

Chen S, Liu Z, Zhu G, Lang K, Ji K, Luo Y, Jin X, Cribb PJ, Wood JJ, Gale SW, Ormerod P, Vermeulen J, Wood HP, Clayton DB (2009) Orchidaceae. In: Wu Z, Raven PH, Hong D (Eds) *Flora of China* (Vol. 25). Science Press, Beijing & Missouri Botanical Garden Press, St. Louis.

Garay LA, Romero-Gonzalez GA (1999) *Schedulae orchidum* II. *Harvard Papers in Botany* 4(2): 475–488.

Huang HX, Chen LJ, Liu ZJ, Li MH (2018) *Liparis vivipara* (Orchidaceae: Malaxideae), a new species from China: evidence from morphological and molecular analyses. *Phytotaxa* 351(4): 289–295. <https://doi.org/10.11646/phytotaxa.351.4.5>

Huelsenbeck JP, Ronquist F (2001) MRBAYES: Bayesian inference of phylogenetic trees. *Bioinformatics* 17(8): 754–755. <https://doi.org/10.1093/bioinformatics/17.8.754>

IUCN (2019) Guidelines for Using the IUCN Red List Categories and Criteria, version 14. Prepared by the Standards and Petitions Committee. <http://www.iucnredlist.org/> [accessed 5 September 2022]

Kumar P, Li J, Gale SW (2022) Integrative analyses of *Crepidium* (Orchidaceae, Epidendroideae, Malaxideae) shed more light on its relationships with *Dienia*, *Liparis* and *Malaxis* and justify reinstatement of narrow endemic *C. allanii*. *Botanical Journal of the Linnean Society* 198(3): 285–305. <https://doi.org/10.1093/botlinnean/boab048>

Li L, Chung SW, Li B, Zeng SJ, Yan HF, Li SJ (2020) New insight into the molecular phylogeny of the genus *Liparis* s.l. (Orchidaceae: Malaxideae) with a new generic segregate: *Blepharoglossum*. *Plant Systematics and Evolution* 306(54): 1–10. <https://doi.org/10.1007/s00606-020-01679-3>

Margońska H, Kowalkowska A, Górnjak M, Rutkowski P (2012) Taxonomic redefinition of the subtribe Malaxidinae (Orchidales, Malaxideae). Koeltz Scientific Books, Koenigstein.

Posada D (2008) jModelTest: Phylogenetic model averaging. *Molecular Biology and Evolution* 25(7): 1253–1256. <https://doi.org/10.1093/molbev/msn083>

Pridgeon AM, Cribb PJ, Chase MW, Rasmussen FN (1999) Genera orchidacearum. vol. 4: Epidendroideae, part 1. Oxford University Press, New York and Oxford.

Ronquist F, Teslenko M, van der Mark P, Ayres DL, Darling A, Höhna S, Larget B, Liu L, Suchard MA, Huelsenbeck JP (2012) MrBayes 3.2: Efficient bayesian phylogenetic inference and model choice across a large lodel lpace. Systematic Biology 61(3): 539–542. <https://doi.org/10.1093/sysbio/sys029>

Stamatakis A (2006) RAxML-VI-HPC: Maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. Bioinformatics (Oxford, England) 22(21): 2688–2690. <https://doi.org/10.1093/bioinformatics/btl446>

Tang GD, Zhang GQ, Hong WJ (2015) Phylogenetic analysis of Malaxideae (Orchidaceae: Epidendroideae): two new species based on the combined nrDNA ITS and chloroplast matK sequences. Guangxi Zhi Wu 35(4): 447–463.

Tian HZ, Hu AQ, Liu QX, Zhou XX, Hu C, Chung SW, Xing FW (2015) *Liparis tsii*: a new species of Orchidaceae (tribe-Malaxideae) from Guangdong, China with its phylogenetic position. Plant Biosystems-An International Journal Dealing with all Aspects of Plant Biology 150(6): 1225–1232. <https://doi.org/10.1080/11263504.2015.1014445>

Ya JD, Lin DL, Han ZD, Cai L, Zhang ZR, He DM, Jin XH, Yu WB (2021) Three new species of *Liparis* s.l. (Orchidaceae: Malaxideae) from Southwest China based on morphological characters and phylogenetic evidence. Plant Diversity 43(5): 401–408. <https://doi.org/10.1016/j.pld.2021.01.006>